DICLIDOPHORA NEZUMIAE SP. N. (MONOGENEA: DICLIDOPHORIDAE) AND ITS ECOLOGICAL RELATIONSHIPS WITH THE MACROURID FISH *NEZUMIA BAIRDII* (GOODE AND BEAN, 1877)*

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ABSTRACT

Diclidophora nezumiae sp. n. is described from the gills of the rat-tail fish *Nezumia bairdii* (Goode and Bean, 1877) taken from the environs of Hudson Submarine Canyon in the northwest Atlantic. The host-parasite relationships were studied in the host population. The new species is most similar to small species of *Diclidophora* having short bodies that taper to maximum width at the level of the first pair of clamps. It may be differentiated from other species by the following: clamps wider than long, noticeably decreasing in size posteriorly; lamellate extension of sclerite *b* does not fuse with sclerite c[1]; unsclerotized diaphragm; a relatively small clamp sucker; 10–13 cirrus hooks; 18–30 intercecal, postovarian testes; unlobed seminal receptacle; filamented eggs; and body dimensions. Of 378 *N. bairdii* specimens examined, 106 (28%) were infected with 1–21 *D. nezumiae* per host. The parasite occurred most frequently on filaments of the first gill arch. Infected fish ranged from 61–428 mm in total length. They were collected at depths of 300–1900 m. Both incidence and intensity of infection were greater for hosts collected between 700–1000 m. Depth of capture of the host was more strongly correlated with fish abundance than with fish size.

INTRODUCTION

Campbell *et al.* (1980) found few species of monogenetic trematodes among the metazoan parasites from 1712 (52 spp.) deep-living benthic fishes taken in the environs of Hudson Submarine Canyon in the northwest Atlantic. Despite examinations of larger (older) fish from depths as great as 5000 m, they found trematodes particularly rare at bottom depths of 2500 m or more, where host populations were low. Most hosts were gregarious and more numerous in shallower habitats. Such relationships were particularly true of *Nezumia bairdii* (Goode and Bean, 1877), infected with a new species of *Diclidophora, D. nezumiae*, described herein. This paper provides additional observations on *D. nezumiae's* occurrence among fish of varying size (age), and on its distribution on the gills of its host and in the host's deep-sea habitat.

In the Hudson Canyon area, *Nezumia bairdii* is the most abundant macrourid

in the shallower and mid-depth regions. But its abundance decreases markedly at depths in excess of 1000 m (Marshall and Iwamoto, 1973; Haedrich and Polloni, 1974; Haedrich, *et al.*, 1980). The species is most common along the Atlantic coast of North America at depths of 90–2285 m. In northern regions it enters cold waters to depths as shallow as 90–183 m, but in lower latitudes it is more common at depths of 548–731 m (Leim and Scott, 1966; Marshall and Iwamoto, 1973).

Materials and Methods

We examined 378 specimens of *N. bairdii* ranging from 5–43.5 cm TL (total length) for parasites and found 347 specimens of *D. nezumiae* sp. n. on 106 infected fish. Hosts examined were as large as any reported (40 cm TL; Marshall and Iwamoto, 1973). Except for the absence of juveniles smaller than 34 mm TL, they represented the complete size range known for the fish species. Fish were collected from most of the species' known depth range (260–1965 m sample range) as part of faunal zonation studies (Rowe and Haedrich, 1979; Haedrich *et al.*, 1980) in Hudson Submarine Canyon (39°13'N; 71°55'W) and adjacent regions of the continental slope and shelf areas. Collecting gear used included semi-balloon, shrimp, or beam trawls.

Helminths were obtained from freshly caught fish, those placed on ice, or from fish preserved in 10% neutral-buffered formalin and transferred to 70% ethanol. Fixing solutions were A.F.A. (alcohol-formalin-acetic acid) or 10% neutral buffered formalin. Whole mounts were stained in Mayer's paracarmine, dehydrated, and mounted in Canada balsam. Type specimens were deposited in the U. S. National Parasite Collection, Beltsville, Maryland, and in the British Museum (Natural History).

A statistical computer package was used to analyze the data (Nie *et al.*, 1975). Intensity data followed a negative binomial distribution and were log transformed to approximate normality. Transformed data were analyzed by linear least-squares regression analysis, one-way analysis of variance, chi-square analysis and the Student-Newman-Keuls multiple range test. Descriptive measurements are expressed as length by width with means given in parentheses. All measurements are in micrometers unless stated otherwise.

Description

Diclidophora nezumiae sp. n. (Figs. 1–5)

Diagnosis: based on 347 specimens, 15 measured. Small worms, broadly triangular in shape, total length 980–2.4mm (1.52 mm) by 420–980 (643) with maximum width at posthaptor. Prohaptor consists of two buccal suckers, 42–61 (50) by 34–53 (41). Opisthohaptor not set off from body proper, bearing four pairs of clamps of unequal size on short peduncles and a terminal lappet. Anterior clamps largest, 76–129 (100) by 106–144 (126); posterior clamps smallest, 72–86 (81) by 80–95 (88); one to three pairs of small hooks sometimes present on terminal lappet. Clamps possess opposable jaws and eight sclerites as described by Llewellyn (1958); lamellate extension b of sclerite a^1 not fused with sclerite c^1, muscular pad over ring formed by sclerites a^2, a^3, b, c^2, c^3; sclerites a^3 and c^3 approach each other medially; d^3 of anterior jaw closely approximating median sclerite a; posterior jaw reinforced by weakly developed riblike thickenings, sclerites g^1 and g^2 rather short and curved to meet sclerites i and k; no lateral flange on sclerite f.

Mouth small, subterminal, ventral. Pharynx 68–117 (102) by 72–91 (85). Esophagus short, intestinal bifurcation just anterior to genital pore. Ceca forming
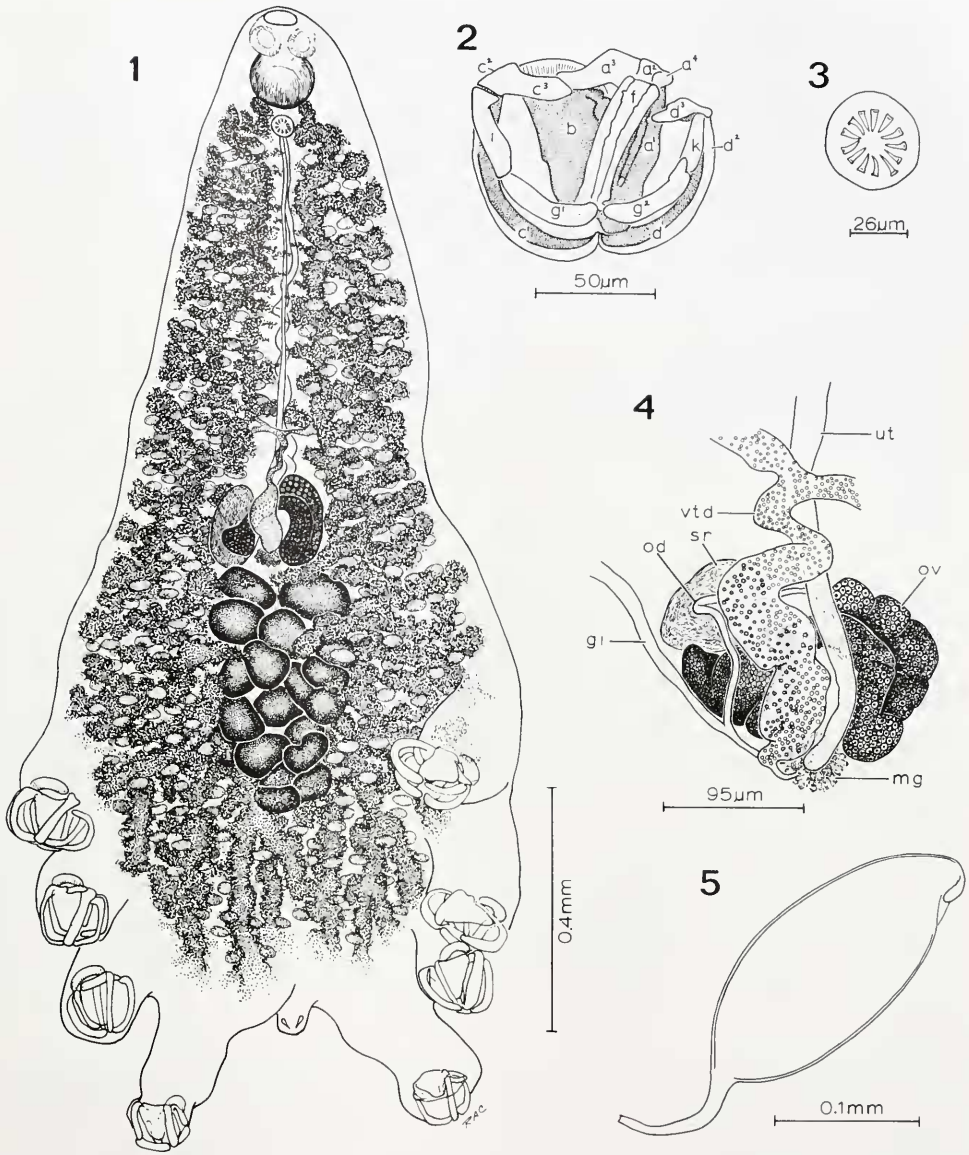
FIGURE 1. *Diclidophora nezumiae* sp. n., holotype. FIGURE 2. Clamp, posterior view. FIGURE 3. Cirrus armature. FIGURE 4. Detail of female reproductive system: gi, genito-intestinal canal; mg, Mehlis' gland; od, oviduct; ov, ovary; sr, seminal receptable; ut, uterus; vtd, vitelline duct. FIGURE 5. Egg, *in utero*.

dorsal and ventral series of medial and lateral diverticula; some diverticula confluent posterior to testes; branches entering posterior extremity but terminating at origins of clamp peduncles.

Testes subspherical or irregular, 18–30 in number, in postovarian median field, entering posthaptor to level of first or second pair of clamps. Vas deferens passing

anteriorly in midline to enter muscular cirrus; cirrus 38–48 in diameter, armed with 10–13 (11) recurved hooks.

Ovary N- or U-shaped, median, in posterior one-half of body. Seminal receptacle and genito-intestinal canal on right side of ovary. Mehlis' gland conspicuous, immediately posterior to ovary. Vitelline follicles small and numerous, coextensive with ceca, not confluent dorsal to testes; transverse vitelline ducts joining in midline just anterior to ovary to form vitelline resevoir. Uterus ascending anteriorly in midline, dorsal to vitelline resevoir, terminating at genital pore. Eggs rarely seen, solitary, filamented, elliptical 216–280 by 72–95 exclusive of filaments.

Systematic relations

Diclidophora nezumiae sp. n. is similar to small species of *Diclidophora* in which the posthaptor is not set off from the body, and which have a triangular body that tapers to maximum width at the level of the first pair of clamps. As might be expected, species most similar to *D. nezumiae* are also from macrourid hosts. Those species are *D. macruri* Brinkmann, 1942, *D. coelorhynchi* Robinson, 1961, and *D. paracoelorhynchi* Mamaev, Parukhin and Zubchenko, 1979. *Diclidophora nezumiae* may be differentiated from these and other species of *Diclidophora* by: 1) short, triangular body not subdivided from the posthaptor; 2) ovary located at midbody to the left of the saccate seminal receptacle; 3) 10–13 cirrus hooks; 4) 18–30 testes confined to the postovarian intercecal space and extending posteriorly to the second pair of clamps; 5) filamented eggs; 6) clamps wider than long and decreasing in size posteriorly; and, 7) unsclerotized clamp diaphragm and lamellate extension *b* not fused with *c*[1] and diaphragm. *Diclidophora macruri*, a species Campbell *et al.* (1980) found on the gills of *Coryphaenoides rupestris* Gunnerus, 1765, differs in having clamps distinctly longer than wide. Morphological differences of *D. coelorhynchi* include its 18 cirrus hooks, and pedunculated clamps in which the diagragm is not quite united with the lateral sclerites or the base of the central sclerite, so that no ring is formed to support the sucker. The general morphology and clamp structure of *D. paracoelorhynchi* are closest to *D. nezumiae*. *D. paracoelorhynchi's* clamp structure is virtually identical in form to that of *D. nezumiae*, except that *D. paracoelorhynchi* has a much larger and more powerful muscular sucker in each clamp than *D. nezumiae* (compare Fig. 1B, Mamaev *et al.*, 1979, with *D. nezumiae*). Furthermore, specimens of *D. paracoelorhynchi* are up to twice as large as *D. nezumiae*, have a lobed seminal receptacle and 40–60 testes.

Of the species of *Diclidophora* from non-macrourid teleosts, *D. phycidis* (Parona and Perugia, 1889), *D. luscae* (Beneden and Hesse, 1863), and *D. esmarkii* (Scott, 1901) resemble *D. nezumiae*. They may be differentiated from the new species in the following ways: 1) *D. luscae* and *D. esmarkii* (morphologically indistinguishable according to Llewellyn and Tully, 1969) have tubercles on the surface of the clamp jaw, para- and postovarian testes and 8–10 cirrus hooks; and 2) *D. phycidis* has many para- and postovarian testes that intrude deeply into the posthaptor (see Llewellyn and Tully, 1969), a well developed sclerotized disc in the diaphragm, an anterior seminal receptacle, unfilamented eggs, and 8–10 cirrus hooks.

Results

Most reports of Monogenea from macrourid fishes have been taxonomic in nature, and, because of the small number of hosts examined, have provided little

information on the ecological interactions between host and parasite populations (see Brinkmann, 1942; Robinson, 1961; Radulescu, 1969; Orias and Noble, 1971; Noble, 1973; Armstrong, 1974; Mamaev *et al.* 1979; Lambert and Euzet, 1980). Earlier reports on Monogenea from macrourids in the genus *Nezumia* listed only unidentified parasites (Radulescu, 1969; Orias and Noble, 1971; Nobel, 1973). Orias and Nobel (1971) found 12 specimens of an unidentified species of Mazocraeoidinae from four *N. bairdii* adults collected off Greenland. Recently, Lambert and Euzet (1980) described a new genus and species of Monogenea (*Polycliphora nezumiae*) parasitic on *N. aequalis* collected near Senegal in the eastern Atlantic.

Regression analysis of fish TL versus depth of capture for the 378 *N. bairdii* specimens examined in this study indicated that fish size increased with increasing depth ($Y = 99.52 + 07.96X$; $r^2 = 0.51$). Because of this "bigger-deeper" relationship, parasite data were analyzed for depth-related and host-size-related differences in incidence and intensity of infection. Table I shows that 28% (106) of the fish were infected with a single species of Monogenea, *D. nezumiae.* A total of 347 *D. nezumiae* specimens were found from fish captured between 300–1900 m, and ranging from 61–428 mm TL.

Incidence

Table I shows incidence data for *D. nezumiae* on fish arranged by 100 m depth intervals. Pooled data (Table II) shows that fish captured between 700–1000 m were more often infected (62%) by *D. nezumiae* than fish taken at other depths.

Comparison of parasite incidence versus host size in each depth zone (Table III) showed that fishes from 700–1000 m had infections more often, regardless of fish size, than those collected from other depths. Larger fishes (>210 mm TL) in every depth zone, except those taken below 1100 m, were more often infected than smaller fish from the same depth zone. Infections were infrequent on all hosts living below 1100 m.

Pooling infection data by fish size regardless of depth of capture (Table IV) indicated that the highest incidence of infection (37%) was in fish ranging from 110–300 mm TL. Immature worms were obtained from seven fish ranging from 83–255 mm TL. Six of these hosts were collected at 500 m and one from 1500 m,

TABLE I

Summary of infection data for Diclidophora nezumiae *on* Nezumia bairdii *collected in the Hudson Canyon area.*

Depth	x̄ Host size (mm)	Examined/ infected	% Infected	x̄ Intensity	No. of worms recovered	No. of multiple infections
300– 400	114	35/10	29	2.8	28	7
500– 600	160	125/44	35	3.0	132	25
700– 800	246	21/12	57	5.2	62	8
900–1000	238	32/21	66	3.3	70	11
1100–1200	249	3/ 2	67	1.0	2	0
1300–1400	305	139/ 9	6	3.6	32	6
1500–1600	304	6/ 1	17	4.0	4	1
1700–1800	190	7/ 2	29	1.5	3	1
1900	324	10/ 5	50	2.8	14	3
Totals		378/106	28	3.3	347	62

TABLE II

Summary of incidence data for Didlidophora nezumiae *on* Nezumia bairdii. *Data from Table I has been pooled for three depth zones.*

Depth	$\bar{x}$ Host size (mm)	Examined/infected	% Infected*
300– 600	150	160/54	34
700–1000	184	53/33	62
1100–1900	300	165/19	12
Total		378/106	28

* Differences in frequency of occurrence were significant ($\chi^2 = 51.71$; $p < 0.01$) for each depth zone.

indicating that *D. nezumiae* is recruited throughout the life of *N. bairdii* in all depths of its habitat.

Intensity

In general, each host harbored an average of 3.3 worms with a range of 1–21 worms among all hosts (Table I). Parasite-free fish and those with only a single monogenean were most common at every depth. Multi-worm infections of *D. nezumiae* occurred on 62 of 106 (58%) hosts, the bulk of them collected from 500–1000 m.

Only a poor correlation ($r = -0.03$) was found between depth of capture of the host and intensity of infection. Also, no significant differences were found when the pooled parasite data were analyzed (one-way ANOVA) from the three depth intervals (Table III). Fishes captured between 700–1000 m had the heaviest average parasite burdens, compared to hosts from other depths.

Significant size-related differences ($p < 0.05$) in intensities were found when

TABLE III

Infection data for Diclidophora nezumiae *on* Nezumia bairdii. *Data for hosts is divided into three size groups from three depth zones.*

Fish size (mm)	# Examined/infected	% Infected	Mean intensity
DEPTH 300–600 m			
50–200	126/33	26	1.85
210–300	28/18	64	4.67
310–375	6/ 3	50	5.33
DEPTH 700–100 m			
70–200	17/ 7	41	1.29
210–300	24/16	67	4.31
310–355	12/10	83	6.30
DEPTH 1100–1900 m			
34–200	8/ 2	25	1.00
210–300	79/12	15	3.33
310–435	78/ 4	5	3.00

TABLE IV

Incidence and intensity of infection of Diclidophora nezumiae *on 378* N. bairdii *specimens grouped into four size classes independent of depth of capture. Fish lengths are total lengths expressed in millimeters.*

	Size class (mm)				
	34–100	110–200	210–300	310–435	Total
Number examined	62	90	132	94	378
Number infected	9	33	48	16	106
Percent infected	14	37*	36*	17	28
Mean intensity**	l44a	1.76a	4.04b	5.12c	3.3
Range	1–3	1–5	1–21	1–16	1–21

* Differences in frequency of occurrence of infections between intermediate-sized fishes and other size-groups were significant ($x^2 = 13.81$; $p < 0.01$).
** Values succeeded by the same letter are not significantly different ($p < 0.05$) (Student-Newman-Keuls multiple range test).

four different size groups of hosts were compared regardless of capture depth (one-way ANOVA; Table IV). Intensity of infection increased with host size.

Size-related differences in intensities of infection were also evident when data were compared within a given depth zone (Table III). In every depth zone the two groups of larger fish consistently had greater numbers of *D. nezumiae* than smaller fishes collected from the same depths. Fishes ranging from 34–200 mm TL were infected by similar numbers of worms regardless of capture depth. Intermediate-sized fish (210–300 mm TL), collected from 300–600 m and 700–1000 m, were infected with similar numbers of worms. The latter parasite densities were considerably greater than those on fishes of similar size taken below 1100 m. *N. bairdii* specimens of more than 310 mm TL taken from 700–1000 m had the highest intensity of infection ($\overline{x} = 6.3$) of any size group examined. Large fish taken from 300–600 m had similar parasite densities, but those taken below 1100 m had only one-half the number of Monogenea per fish compared to those from 700–1000 m.

Microhabitat

Data on microhabitat of *D. nezumiae* collected from 28 hosts are presented in Tables V–VI. Since chi-square analysis indicated no significant differences ($p > 0.30$) between number of infections of arches on right or left sides, data from

TABLE V

Distribution of Diclidophora nezumiae *on the gill arches of* Nezumia bairdii *(Percent occurrence in parentheses; number of hosts = 28).*

	Gill arch					
	I	II	III	IV	Unknown	Total
No. worms—right side	17(22)	8(10)	1(1)	10(13)	6(8)	42(53)
No. worms—left side	22(28)	4(5)	2(2)	6(8)	3(4)	37(47)
Total	29(49)	12(15)	3(4)	16(20)	9(11)	79(100)

TABLE VI

Distribution of mature and immature Diclidophora nezumiae *specimens on particular gill arches and hemibranchs of* Nezumia bairdii *(Percent occurrence in parentheses).*

	No. of worms	Gill arch				No. of worms	Hemibranch		Gill Arch Position	Incidence	
		I	II	III	IV		Outer	Inner		Mature	Immature
Mature	57	33(47)	7(10)	3(4)	14(20)	54	42(63)	12(18)	Dorsal	16	3
Immature	13	6(9)	5(7)	0(0)	2(3)	13	5(8)	8(12)	Middle	9	2
Total	70	39(56)	12(17)	3(4)	16(23)	67	47(70)	20(30)	Ventral	7	2

both sides were pooled. The dorsal one-third of gill arch I was most often infected and was the site selected by most of the mature and immature worms (50% of total). Gill arches II and IV were each infected 11 times with similar numbers of worms, and gill arch III was the least often and least heavily infected site (χ^2 = 9.43; $p < 0.05$). Mature worms were more often observed attached to the outer (anterior) hemibranchs than the inner (posterior) ones, but immature worms were distributed evenly between the hemibranchs. All worms attached to a single primary lamella in a manner similar to that described for *D. luscae* (Llewellyn, 1956).

DISCUSSION

Parasite populations, particularly those which do not use intermediate hosts in their life cycles, are especially susceptible to variations in their hosts' population densities. Examination of the distribution of infections by *D. nezumiae* on *N. bairdii* revealed that interactions of parasite and host populations varied with capture depth and host size.

Nezumia bairdii has a "bigger-deeper" distribution in the Hudson Canyon area (Polloni *et al.*, 1979; Haedrich *et al.*, 1980). Within this area, these fish occurred in three distinct depth zones. In the shallowest zone (300–600 m), the *N. bairdii* population was predominantly smaller fish ranging from 50–160 mm TL ($\bar{X} = 150$ mm TL). The second zone, 700–1000 m, was inhabited mainly by intermediate-sized fishes, 170–300 mm TL ($\bar{X} = 184$ mm TL). The third depth zone, 1100–1900 m, was inhabited by large fish, usually >250 mm TL ($\bar{X} = 300$ mm TL). Haedrich *et al.* (1980) and Marshall and Iwamoto (1973) noted that *N. bairdii* decreases in abundance below 1000 m. As noted earlier, within the Hudson Canyon area the center of abundance for *N. bairdii* lies between 500–1000 m.

In view of the dispersion of the different size groups of *N. bairdii,* it was not surprising to find different incidences of parasitism by *D. nezumiae* on hosts collected from different depths. Analysis of the infection data (both incidence and intensity) showed that the highest levels of parasitism by *D. nezumiae* occurred on fish collected from 700–1000 m, the depth zone corresponding to the center of abundance for *N. bairdii* in this region (Haedrich *et al.*, 1980). Each of the three size groups within this depth zone was infected more often and usually harbored greater numbers of worms per fish than their counterparts captured at other depths. The high levels of infection in fishes collected between 700–1000 m indicates that this depth zone is also the center of abundance for *D. nezumiae.* Hence, the success and abundance of *D. nezumiae* depends directly upon the host population density.

Host-size was secondary in importance to depth-related differences in host population densitites in influencing infections of *D. nezumiae.* Only fishes smaller than

60 mm TL were completely free of monogeneans. All other size groups harbored *D. nezumiae,* but in numbers varying with host size. The smallest *N. bairdii* specimens (34–200 mm TL) had the lowest infection rate (14%) and, with one exception, harbored the fewest worms per fish ($\bar{x} = 1.6$ per host) of any size group examined. Low intensities of infection may be expected in these smaller fish because they were collected mostly in depths less than 700 m (shallower than the center of abundance of *N. bairdii*) and because the smallest of these fishes probably represented recent recruits settling from overlying waters. New recruits evidently had not had sufficient time to develop infections of *D. nezumiae.*

Intermediate-sized fish (210–300 mm TL), exception in one depth zone, had the highest infection levels of all those we examined. The exception was in the 700–1000 m zone, where fish >310 mm TL had higher frequencies and intensities of infection. The high levels of infection in the intermediate-sized fishes was expected because a major proportion of these fishes were collected between 700–1000 m, the center of abundance for *D. nezumiae* (Table III).

The largest fish (310 mm TL) were taken mostly below 1000 m. Only 18 of 96 individuals from this size group were collected from depths less than 1100 m. Both incidence of infection and intensity per infection were lower in this size group than in the intermediate-sized fishes. In the deepest area, where 81% of the largest fishes were collected, only 4 of 78 (5%) were infected.

Diclidophora nezumiae had a preferred site of attachment: both adults and immature worms preferred gill arch I. Mature worms preferred the dorsal one-third of the outer hemibranchs, but immature worms were almost evenly distributed between the hemibranchs. Gill arches II and IV were also occupied by mature and immature monogeneans, but to a lesser degree. Where attachment site information was available for other species of *Diclidophora,* only three of six species (*D. denticulata* Rees and Llewellyn, 1941; *D. macallumi* Price, 1943 and D. merlangi (Kuhn, 1832)) were found most often on gill arch I.

Monogeneans' attachment sites are related to a variety of physical and physiological factors. Among these are the host's ventilating mechanism and immune responses, the parasite's mobility, and intraspecific competition among monogeneans (Suydam, 1971). It is not known which of these factors influence the distribution of diclidophorids on their macrourid hosts, but intraspecific competition seems unlikely, as macrourid infections typically involve only a few specimens of Monogenea. In fact, their most likely metazoan competitor upon the gills of macrourids would be parasitic copepods.

This study shows that factors which influence the success and abundance of infection of monogeneans in shallow-water fishes, such as host population density, distribution, and size, also influence the degree of infection attained by monogenetic trematodes in slope-dwelling fishes such as *N. bairdii.*

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